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NOTES ON THE ANATOMY OF THE PUNCTATUS GALL.

ALBAN STEWART

Our knowledge of the anatomy of Cynipid galls is based largely upon the investigations of Beyerinck, Hieronymus, Küstenmacher, Küster, Lacaze-Duthiers, Prillieux, and Weidel, but as the publications of these various authors have to do mainly with other than American galls, our knowledge of the anatomy of these remains meager for the most part.

During the summer of 1913 I was fortunate enough to discover a tree of the black oak, *Quercus velutina* Lam., in the western part of the state of Missouri, the smaller stems and branches of which were covered in places with galls caused by *Andricus punctatus* Bass. As there were galls on this tree in different stages of development, I collected a series and preserved them for further study. The galls caused by this insect are rather striking in appearance as they form knot-like swellings on the branches, which sometimes attain a diameter of five or more centimeters. The most of them, however, are smaller than this. They may occur singly, or two or more of them may be closely associated, one above the other on the same branch, which may become joined together by subsequent growth so as to appear as one gall. When they occur close together on the same branch, in the earlier stages of their development, the smaller galls are usually located towards the distal end.

The larger galls are roughened on the outside and are covered with small openings about 1 mm. in diameter, each of which leads into an empty larval chamber (fig. 10). Each opening is usually surrounded by a circular area, about 3 mm. in diameter, in which the surface of the bark is smoother and lighter in color than elsewhere. The openings persist for quite a while after the chambers are vacated, but they may ultimately become more or less obliterated by the subsequent growth of the gall. The larval chambers extend inward from the openings in a direction usually more or less perpendicular to the outer surface (fig. 2), so that cross sections of older galls will generally show various views of different chambers in the same section.

It is very evident that these galls may continue to grow for several

years. The largest one in the collection has a cross-diameter of 6 cm. while the apparently normal stem just above it has a similar diameter of 1.6 cm. This portion of the stem has eight annual rings of growth, while the gall has but one ring of growth next to the pith which is normal, the rest of them being greatly altered in their structure. The second ring of growth from the pith shows less alteration than does the woody tissue outside of it. Its outer boundary is plainly marked, and, so far as one can judge by examination with a hand lens, it differs structurally from a normal ring of growth in having greater width and broader rays. The tissue outside of this shows no indication of annual rings except just inside the cambium where such a ring is differentiated in places. Another smaller gall examined has a diameter of 3.4 cm. and two apparently normal rings of growth at the center, while the stem just above it has a diameter of 8 mm. and five rings of growth. The tree from which the galls were taken has been infested with them for many years according to the inhabitants of the region. Similar galls are caused by this insect on *Quercus coccinea*, *Q. ilicifolia*, *Q. nigra*, and *Q. rubra* according to Cook (5, p. 28).

It is rather difficult to locate galls of this kind in their earliest stages as there is usually no external evidence of them beyond a slight swelling of the bark¹ such as might result from other causes. A cross section of an early stage is shown in fig. 1. The bark is about twice as thick on the side where the gall is located as it is on the opposite side of the stem, but there is practically no increase in the thickness of the wood. Apparently the first effect of the gall stimulus is to cause the formation of a larger amount of bark tissue than normal. Outside of the increase in the thickness of the bark no other striking abnormalities appear in the neighborhood of the gall.

The larval chamber is not as well defined as it is in later stages of development. The cavity containing the larva is irregular, conforming roughly in shape to it. The protecting layer of stone cells, somewhat lightly colored in fig. 1, is semilunar in outline and is only developed on the outside of the chamber in the section shown. Higher up in the same series of sections, however, a complete ring of stone cells has been formed. Just below the cavity, shown in fig. 1, there is a radial segment of brown-colored parenchyma cells which extends from the base of the cavity to a slight depression in the cork layers covering the gall on the outside. This segment is surrounded by

¹ The term bark is used to include all tissues located outside the cambium.

several layers of cork cells, and it is possible that it has resulted from the sting of the insect in depositing the egg in the bark, as no other causal evidence is shown. Küster (13, p. 187) states, however, that wound-cork does not result from such action but callus tissue instead.

There has been no increase in the formation of wood near the gall at this stage if a slight protuberance on the lower left hand side of the chamber in fig. 1 be excepted. In fact the production of woody tissue has been somewhat inhibited at the base of the chamber. A mass of parenchyma has been formed here, the cells of which have thin un-lignified walls. Later the walls of these cells thicken and lignify resulting in the condition shown in fig. 3. A few short scalariform tracheids and other lignified elements are scattered among these parenchyma cells, very much disarranged in their positions.

In the stage of development shown in fig. 1, all of the chamber is surrounded by bark tissue except the inner side of it. A later stage (fig. 2) shows the inner part of a chamber to be embedded in woody tissue. The way in which this comes about can be studied to best advantage in serial sections cut tangentially through the gall. Usually the first woody tissue to appear, in the outermost sections of such a series, is small irregularly arranged masses, which, in sections a little further in, take roughly the form of small fibrovascular bundles (fig. 4). In this figure a small portion of the protecting layer is shown on the lower side. These pseudo-bundles sometimes join directly one with the other, or distinct ray-like masses of parenchyma and other cells may occur between them. The bundles often extend but part way around a chamber, other parts of it being surrounded by irregularly arranged masses of wood cells. Longitudinal sections through a chamber often show these bundles extending parallel with it in the bark covering of the gall. They are composed largely of bands of scalariform tracheids. Numerous galls have been examined in this regard and the bundles have always been found to be present to a greater or less extent. They are confined to the bark and thus form only the outer part of the woody covering of the chamber. The inner portion of the larval chamber is surrounded by woody tissue formed by the cambium. Soon after the gall starts, the cambium ceases its activity at the base of the chamber while it is stimulated to greater growth along the sides. The first stage of the enclosing process is shown in fig. 1, where a slight woody projection has formed at the lower left-

hand side of the chamber. By further growth of the cambium a condition comes about like that shown in fig. 5, in which the wood has been formed well around the base of the chamber. The final result of this process is shown in fig. 2, where the inner third of the chamber is surrounded by wood. The enclosing method here outlined is somewhat similar to that described by Mäule (15, p. 24), where woody bodies, formed in the bark of wounded stems of *Salix phylicifolia*, are gradually surrounded by the activity of the cambium forming wood around them.

After a larval chamber is vacated by an insect the opening to the outside remains for some time. It is possible to stick a dissecting needle into the openings in some of the older galls for a distance of 1.5 cm. or more, and longitudinal sections through such chambers show that they may extend in nearly to the normal wood around the center which was evidently formed before the gall started. Sometimes the openings can still be seen several years after the cavity was vacated but after a time they may become closed and more or less obliterated by the growth of the bark around them.

A longitudinal section through a chamber recently vacated by an insect is shown in fig. 2. The chamber is lined with several layers of stone cells which, however, do not extend to the periphery of the gall. The thin-walled parenchyma cells, which fill the outer portion of the chamber before the insect emerges, have been largely destroyed in the section figured, and can only be seen to the right and left just inside the opening. In earlier stages, before the insect comes out, the stone cells extend inward from the periphery toward the center of the chamber and form a loosely arranged arch across it a short distance inside the opening. The loose arrangement of these cells offers but little resistance to the insect in leaving the chamber. Outside the protecting layer and running parallel with the sides there is a corky covering composed of several layers of cells, shown by a light line on each side of the chamber in fig. 2. It is probably somewhat similar to the corky covering around the protecting layer in the stem gall of the oak described by Lacaze-Duthiers (14, p. 338). It is not always the case that the protecting layer extends entirely around the chamber, as the inner end and sides of it may join directly onto the wood in these places.

If the protecting layer is examined in a longitudinal section through a chamber, it will be noticed that there are in general three kinds of

stone cells which compose it. There are stone cells which are isodiametric or nearly so, and others which are much elongated in one direction, the last of which have their long axes arranged parallel with the chamber. There are still other stone cells which are more or less intermediate between the two kinds just mentioned, in which one diameter is somewhat longer than the other. Sections cut across a chamber sometimes show that these intermediate cells are arranged with their long axes perpendicular to it. It is evident that both isodiametric and elongated stone cells make up the protecting layer of this gall. There is a great difference in the thickening of the walls of the stone cells. Some have very thick walls with well-marked pits and small lumina, while others have thin walls and large lumina. Furthermore it is possible to find, among these, cells which have the walls unequally thickened on different sides, and which are very similar to those described by Weidel (21, pp. 329-330). Such cells do not occur in the normal parts of the oak, according to this author, but they do occur normally in certain members of the *Rosaceae* according to Küster (12, p. 183). Weidel found still further that stone cells with one sided thickening of their walls were confined largely to leaf galls in the forms studied by him. He also makes some interesting comparisons between the stone cells in Cynipid galls and those which occur normally in the oak. He finds that isodiametric stone cells are the ones that commonly occur in the normal parts, those which are elongated in one direction being confined to the bud scales and reproductive parts. It might be well to mention in this connection that Küster (12, p. 181) has found that the palisade-like stone cells with large lumina which occur in the gall of *Hormomyia fagi* call to mind similar cells that occur in the beech cupule. As elongated stone cells occur in the reproductive parts of the oak and related forms, one is led to suspect that possibly this kind of stone cell may be more primitive in the oak than the isodiametric form, since primitive characters are likely to persist in these parts. This supposition is strengthened by the fact that this kind of stone cell reappears in many oak galls so that the ability to form them must be latent and is only awakened to activity through the action of the gall stimulus. Such may be true of the ray structure to be considered further along in this article.

In young normal stems of this species of oak the stone cells of the bark are arranged in one or more concentric layers. Groups of stone cells may also occur opposite the broad rays, which are connected

with one of the layers just mentioned. In the early stages of development of the gall this layered arrangement of the stone cells is not greatly interfered with, but in later stages the layers are broken up resulting in irregular masses scattered through the bark which are composed of stone cells larger than those normally present. The lumina of many of these contain a yellowish-brown substance which gives a strong reaction for tannin. They are evidently the same as the tannin balls described by Hartwich (10, pp. 147-149). Similar tannin accumulations also occur in other cells of the bark as well as in the cells of the protecting layer.

Corky inclusions occur quite commonly in the bark of the gall, which surround either groups of parenchyma or stone cells. One of these bodies is shown in fig. 7, where the cork forms a light colored circular figure at the center of the photograph. Mäule (15, p. 24) mentions cork growths in the bark of wounded stems but in these instances the cork is surrounded by a woody mantle composed of wood parenchyma cells and short tracheids. Groups of irregularly arranged tracheal elements also occur in the bark of the gall, the tracheids which compose them being short, sometimes nearly isodiametric, with scalariform markings on their walls. These may be arranged as single strands, or groups of tracheids may be associated together which are connected with similar groups a short distance away by cross bridging. The arrangement of the elements is often very complex resulting in twisted masses of tracheids as is shown in the center of fig. 6. Parenchyma cells sometimes occur in these tracheal complexes in the bark, the arrangement of which suggests narrow rays. Somewhat similar bodies are found in the bark of the black knot gall on *Prunus virginiana* (see Stewart 20, p. 120). Small groups of parenchyma cells may become partially surrounded by a woody growth in such a way as superficially to resemble the cross section of a sector of a small dicotyledonous stem, the parenchyma around which the woody growth takes place corresponding in position to the pith of such a stem. Some of these woody bodies have a cambium and seem to be capable of further growth.

But little is known about the origin of these peculiar woody bodies which occur in the bark. Mäule (15, p. 24) found special ball-formations² and other woody growths in the bark of wounded stems but

² The term "Knäuel," used in the German literature to designate these peculiar woody growths, is rather difficult properly to express in English. Miss Frances

was unable to explain their origin. It is evident that he searched carefully for the beginning stages of such but did not succeed in finding them. Krick (11, p. 17) has also found somewhat similar bodies to be normally present in the bark of the red beech, some of which had cork for a central nucleus while still others had wood. It is possible that many of these woody complexes in the bark may originate from misplaced cambium cells. Such is evidently the case in the galls caused by the black knot fungus on the choke-cherry (Stewart 20, pp. 119-120).

With the possible exception of the pine, it is likely that the structure of no wood is better known generally than that of the oak, as both of these woods are usually studied in elementary courses in plant histology in institutions where such courses are offered. The results of a large amount of investigation have been published on the structure of oak wood but to attempt to enumerate all of these would be superfluous in this article. Hartig (9, pp. 92-96) gives a rather detailed account of the structure of this wood, and Bailey (2 and 3), Bailey and Sinnott (4), and Eames (7), treat the ray structure rather exhaustively.

Normal oak wood is composed of vessels, tracheids, fibers, and parenchyma cells, the last of which occur both as wood and ray parenchyma. The vessels are very large and there is a tendency for them to form scalariform perforations according to Solereder (19, p. 781). In some species, especially those belonging to the white oak group (subgenus *Lepidobalanus*), the vessels become filled with tyloses after a time. Gerry (8, pp. 451, 455-456) has recently done some work on the subject of tyloses and finds that in contrast with the white oaks the members of the red-oak group (subgenus *Erythrobalanus*) are normally free from tyloses with many exceptions. Tyloses occur scattered or frequent in the sap wood of *Quercus velutina* and scattered in the heart wood. In the closely related scarlet oak *Q. coccinea* they are usually scattered but may be abundant in connection with fungus growths. The formation of tyloses is easily induced through the wound stimulus. Gerry (8, p. 447) found that even the wound produced by felling the tree may cause the formation of tyloses in the outer rings of *Q. michauxii*.

Dorrance, who is completing a translation of Küster's *Pathologische Pflanzen-anatomie*, has been kind enough to supply me with some of her translations of this and closely related terms. Among these are: knarl, ball, and ball-formation.

Specimens of a number of the normal branches were taken from the tree from which the galls were collected to be used in comparing the normal wood with that of the gall. Without exception these specimens show tyloses to be present in the vessels, and their abundance in places leads one to suspect that they may not all have been normally produced. Possibly the gall stimulus has had something to do with their production. I have been unable to find any references in the literature on the anatomy of galls which records exactly similar conditions, but it seems to be an established fact that the stimulus resulting from parasitic fungi is capable of exerting an influence upon the structure of the host plant some distance beyond where the fungus actually occurs. The normal wood of *Abies* contains no resin canals, but Anderson (1, p. 465) found them to be present in all branches above parts infected with *Aecidium elatinum*. He also found (pp. 473, 476) that the branches of *Pinus Strobus*, *Larix japonica*, and *Picea excelsa*, which were situated above parts infected with *Agaricus melleus*, contained a greater number of resin canals than did the normal wood of these species. Mer (16, p. 367) also states that resin canals occur in the branches of *Abies pectinata* which are above parts infected with *Phoma abietinae*. Rather striking abnormalities may result from the wound stimulus some distance away from the actual wound. Mäule (15, p. 12) found in *Rosa centifolia* that very broad rays and short wood cells persist 5-6 cm. from the wound, and De Vries (6, p. 20) found evidences of wounding in the structure of the wood of the *Caragana aborescens* 7 cm. from the wound. The above citations give sufficient ground for believing that if the tyloses in the branches of this oak result abnormally, the gall stimulus is the cause of it.

The origin and structure of the broad rays in oak wood has been the subject of much study and discussion in recent years. As is well known, the rays in oak wood are of two kinds: those which are one cell wide in cross and tangential section, known as uniseriate rays, and those which are more than one cell wide. The rays of the second group can be further subdivided into those which are 2-3 cells wide, multiseriate, and broad homogeneous plates of parenchyma tissue, or compound rays. Of these three kinds, the uniseriate rays are usually considered to be the more primitive.

Until rather recently the broad rays, the so-called primary medullary rays, have been considered to be inclusions of the fundamental tissue between the primary fibrovascular bundles. In his study of

the structure of the wood of fossil oaks from the Miocene of California Eames (7, pp. 161-163) found uniseriate rays in his sections, but none of the broad homogeneous rays, their place being taken by groups of narrow rays aggregated together. Eames also studied the wood structure of a number of seedling oaks and found in the group of black oaks, to which *Q. velutina* belongs, that the first broad rays formed were similar in structure to those in the fossil oaks. He found still further that the homogeneous rays come about through a loss of the fibers, etc., in the aggregations of narrower rays, so that the compound rays of adult wood are formed after a time by this means. In the group of white oaks he found a still more primitive condition in the seedling as only uniseriate rays occur for a foot or more above the ground and extending through 15-20 annual rings of growth. The broad rays of the mature wood arise by aggregation and fusion of the narrow rays in the manner just stated.

Our knowledge of the structure of the oak ray was still further advanced by the work of Bailey (2), who found in his studies of traumatic oak wood, that the rays formed immediately after wounding were all uniseriate. By aggregation and fusion of these the normal compound rays result again in subsequent layers. His results seem to show that the ancestral conditions of ray structure are possibly recapitulated in wounded areas. In a later paper, however, Bailey and Sinnott (4) 46, state that seedling stems and roots of *Quercus alba*, which possess only uniseriate rays, will form wide multiseriate rays after injury, often without indication of the putative stages of compounding.

In the examination of tangential sections of this gall I found rays which were similar in many respects to those figured by Bailey (2, pl. XI, fig. 2). In fact a large number of the broad rays in different galls showed an inclusion of fibers and other elements to a greater or less extent, but usually not so strongly marked as in the ray figured by Bailey. This condition led to the supposition that possibly a repetition of the conditions described by Eames and Bailey might take place in their formation. In order to determine whether this supposition was true or not, one of the smaller galls was selected, and tangential sections cut of it from the outermost layers of gall wood to the normal wood inside, formed before the gall started. A larval chamber was located on this side of the gall, and the section were cut at right angles to its long diameter as shown in fig. 2. Every other section was mounted in glycerine and preserved in series for study.

The first rays to appear in the outermost sections of this series are narrow for the most part, usually 1-4 cells wide. There are occasional rays, however, which are somewhat wider but none so wide as those which occur in sections taken farther in. A little deeper in the gall wood many of the rays broaden and occasionally there is a very wide one in which there are inclusions of fibers. Some of the ray combinations in this region are quite similar to the traumatic ray of *Quercus nigra* figured by Bailey (*l. c.*). Each succeeding group of a few sections towards the interior of the gall shows a broader zone of wood around the larval chamber. With the increase in the amount of wood, many of the rays also increase in width until they reach the size shown in fig. 8. Some of these rays have inclusions of fibers as is shown in the figure, while others are practically free from such. Uniseriate rays also occur here among the fibers, etc., which lie between the broad rays.

By examination of sections still deeper in the gall from those shown in fig. 8, a condition is finally reached in which the rays are practically all uniseriate. This condition is shown in fig. 9, which was taken from a part of a section corresponding closely in position with that shown in fig. 8. It is further evident that the section shown in fig. 9, was of gall wood and not of normal wood, which occurs a short distance inside, because there is a parenchymatous area to the right, not shown in the photograph, which was located near the base of the larval chamber. It is similar in structure to the part shown in fig. 3 which was taken from near the base of the larval chamber of this same gall. The section from which fig. 9 was taken also includes some of the stem just below the gall, a portion of which is shown in fig. 11. The structure of the wood is nearly normal in this portion and it is interesting to follow the broad rays from the part of the section shown in this figure, to the part shown in fig. 9, as they gradually break up into smaller ones by fiber inclusions as the section through the gall is approached.

We have here a rather striking correlation between the effects produced by the gall stimulus and those which come about after wounding, as the results are very much the same in each case. There is this difference, however, that after the formation of the broad rays, they may break up or be replaced by narrower ones farther out in the gall. If such a condition exists in traumatic oak wood it is not mentioned by Bailey. The reversion to a supposedly primitive ray structure in each instance is rather striking.

There are still other interesting things to be noticed in the ray structure of this gall. The broad rays, mentioned in the preceding paragraph, are more or less fusiform as a rule when seen in tangential section, and are much shorter vertically than in normal wood. De Vries (6, p. 83) also found a vertical shortening of the rays in primary wound wood. Between the pseudo-fibrovascular bundles, which form the outer part of the woody covering around the larval chambers, there are often ray-like structures present which are composed of several layers of unligified parenchyma cells (fig. 4) radially arranged with reference to the chambers. Raylike bodies sometimes appear between these bundles, which on closer examination are seen to be composed of short scalariform tracheids turned over so that their long axes are presented. There are often large areas within the gall composed of ray-like cells but which are too irregular in shape to be considered as rays (fig. 3). Somewhat similar areas occur in traumatic wood of this species of oak.

From what has been said concerning the ray structure in the preceding paragraphs one would conclude that the course of the fibers and other elements would differ greatly from normal in the wood of the gall, and such is the case. In places where broad rays occur the fibers and other cells of the wood are very much bent from their usual upright course to conform to the shape of the rays. Individual strands of fibers or groups of them often pursue a very irregular course through them (fig. 8). In places where there are a number of closely associated multiseriate rays the course of the fibers surrounding them is often wavy. The complexity of fiber arrangement is often so great as to result in true ball formations as is shown in fig. 13. Mäule (15, p. 9) has done some work on these peculiar fiber arrangements and concludes that they come about to a great extent through the attempt of the young wood cells to reach their normal length when they meet with resistance in their growth. According to Mäule the young wood cells can bend in three directions, either outward radially, or to right and left tangentially. They never bend inward because the older wood lies in this direction. Their usual course of bending is to right and left so that they are generally seen in tangential sections. They occur but seldom in this gall but when they do appear they are always in tangential sections.

There is a great disturbance in the course of the fibers around the larval chambers and around the masses of lignified parenchyma cells

which occur near the bases of such. There is often a parting of the fibers to right and left tangentially in such regions, a condition which is still apparent for some distance above and below a chamber. Mäule (15, pp. 19-20, pl. 1, fig. 8) describes and figures a somewhat similar arrangement of fibers in the wood formed in a direct line with longitudinal wounds on stems of *Cornus sibirica*. The structure of the masses of lignified parenchyma, which occur around the bases of the larval chambers (fig. 3) are very complex and no regular arrangement of the cells can be distinguished. The cells in such places are mostly short and are not dissimilar to the short-celled elements which are formed immediately after wounding. Fibers are sometimes mixed with the parenchyma cells in which case they pursue a very irregular course. Mäule (15, p. 7) mentions conditions somewhat similar to this near wounds on stems of *Caragana*, *Abies*, *Aesculus*, *Salix*, and *Tilia*.

The course of the cells in the wood appears to be nearly normal in most places in cross sections of galls as the greater part of them are not so greatly bent from their upright course as to be readily apparent in such sections. There are places, however, in which the course of the cells is very much altered, and small segments of the wood may be turned over nearly at right angles so that the long axes of the cells are presented. Such an arrangement is shown in the lower right hand side of fig. 14. In places of this kind the shortness of the cells which are turned over is very apparent. The change in direction of the cells from vertical to horizontal or nearly so, is usually sudden and there are seldom pronounced transitional stages between. Cross sections also show a great reduction in the number of vessels, and where the disturbance has been greatest, an entire absence of them. They occur more commonly in the gall wood first formed, from which narrow vessel-containing segments may extend outward into wood from which they are otherwise absent (fig. 12). Sometimes the narrow vessel-containing segments extend nearly to the cambium. In traumatic wood of these species of oak, formed soon after wounding, there is a great reduction in the number or an entire lack of vessels.

In cross sections of many of the older galls a layer of wood has been formed just inside the cambium which is normal in many respects (figs. 5 and 14). This layer sometimes extends through nearly the entire circumference of the gall, but more often only segments of it occur. The cells in this layer usually have nearly their normal

arrangement and associations. Large vessels appear which do not occur in the wood just inside of it. Occasionally small segments of this layer are turned over showing that the cells which compose it are shorter than normal. The layer as a whole is as sharply set off from the wood inside as are two annual rings of growth. It looks very much as if there is here a suggestion of a return again to normal growth. It is a well known fact that after a time the cambium returns to its normal functions in wounded areas, after the wound is healed.

In radial sections through galls the most of the tissue presented is ray tissue. Owing to the fact that so many of the fibers are bent to right and left tangentially, but few entire ones appear in such sections, as the most of them have been cut across. One often finds in the vicinity of larval chambers in these sections what appears to be a nearly true cross-section structure of wood (see lower left hand side of fig. 2). Such areas are made up mostly of fibers.

Tannin bodies, similar to those which occur in the stone and other cells of the bark, also occur in many of the cells of the wood. These bodies may completely fill the lumina of the cells or only partly so. They are either homogeneous or granular in appearance.

In concluding this article it seems desirable to summarize briefly the important facts contained in it. The presence of elongated stone cells in the protecting layer around the larval chambers is a fact of some interest as these cells occur normally in no others part of the oak than the bud scales, and in the reproductive parts, the last of which is an important place for the retention of primitive characters. The presence of stone cells in the protecting layer with unequally thickened walls is another fact of interest, as such cells do not occur normally in the oak. They are usually confined in their distribution to the leaf galls on it.

The following conditions in this gall can be correlated with similar conditions in traumatic tissue:

1. A recapitulation of similar conditions of ray structure.
2. A vertical shortening of the broad rays.
3. The presence of ball-formations in the wood, which appear only in tangential sections.
4. A parting of the fibers in the vicinity of the larval chambers, similar to the condition resulting from longitudinal wounds.
5. Isodiametric parenchyma cells around the base of the larval chambers with irregularly distributed fibers and other woody elements among them.

A great reduction in the number, or an entire lack of vessels.

7. A shortening of many of the cells of the wood.

8. Absence of distinct annual rings of growth.

9. A suggestion of the return of the cambium to normal activity after a time.

10. Woody inclusions in the bark.

The fact that similarities often exist between the structure of galls and traumatic tissue is well known among workers in pathological plant anatomy. Küster (13) mentions this fact in several places in his work. Possibly one of the most noteworthy single examples of this kind is that mentioned by Molliard (17, p. 200) in which by pinching the buds of *Pelargonium zonale* structures were produced similar to those in the flower galls on *Geranium dissectum* caused by *Cecidophyes Schlechtendali*. I believe, however, that this is the first time that the conditions in a single gall have been correlated with the conditions in traumatic tissue in so many important ways. The comparisons made with wound tissue in this article have been based largely upon the general results of De Vries and Mäule. I hope, however, to continue further this investigation on other woody oak galls, and to compare more closely the structure of the gall wood with that of traumatic wood of the oak.

METHODS

The galls used for sectioning in this work were preserved in a weak solution of formaldehyde when they were collected and left in it until they could be further treated. In order to prepare sections for study, the galls were first macerated to remove the formaldehyde, and were then placed under the receiver of an air-pump and the air exhausted until bubbles ceased to rise from them. They were then transferred to strong hydrofluoric acid and left for about two months in order to remove all of the mineral matter. No difficulty was experienced in cutting sections less than $10\ \mu$ in thickness except that large sections, cut thinner than this, were badly broken up in the subsequent handling. Sections $10\ \mu$ in thickness were used in most instances as they were found to be sufficiently thin for all that was required.

An alcoholic solution of safranin was employed for staining, and as a counter stain "licht Grün" dissolved in clove oil was used. This had the double advantage of both counterstaining and clearing

the sections. Iron-alum haematoxylin was tried as a counter stain, but owing to the large amount of tannin in the galls, it was not a success. Where serial sections were necessary they were cut somewhat thicker as a rule and mounted in glycerine. Such of these as were required for close study or photomicrographing were removed from the series, stained, and mounted separately.

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MADISON.

SUMMARY OF LITERATURE CITED

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DESCRIPTION OF FIGURES IN PLATES LI AND LII

All figures are of the Punctatus gall from *Quercus velutina*.

PLATE LI

FIG. 1. Cross section of a very young gall showing larval chamber. $\times 13$.

FIG. 2. Longitudinal section through a larval chamber shortly after it has been vacated by the insect. $\times 9$.

FIG. 3. Tangential section through an old gall showing a portion of the complex of isodiametric parenchyma cells near the base of the larval chamber. $\times 33$.

FIG. 4. Tangential section showing pseudo-fibrovascular bundles around a portion of a larval chamber. A part of the protecting layer is shown on the lower side of the figure. $\times 33$.

FIG. 5. Tangential section through a gall showing a larval chamber being enclosed by woody tissue. Intermediate between the stages shown in figs. 1 and 2. $\times 9$.

FIG. 6. Woody inclusion in the bark of the gall. Light colored body at center of figure. $\times 33$.

FIG. 7. A cork inclusion in the bark of the gall. Light area surrounding the center. $\times 33$.

PLATE LII

FIG. 8. Tangential section through outer woody covering of gall showing uniseriate and compound rays. $\times 33$.

FIG. 9. Tangential section through central portion of gall showing only narrow, mostly uniseriate rays. $\times 33$.

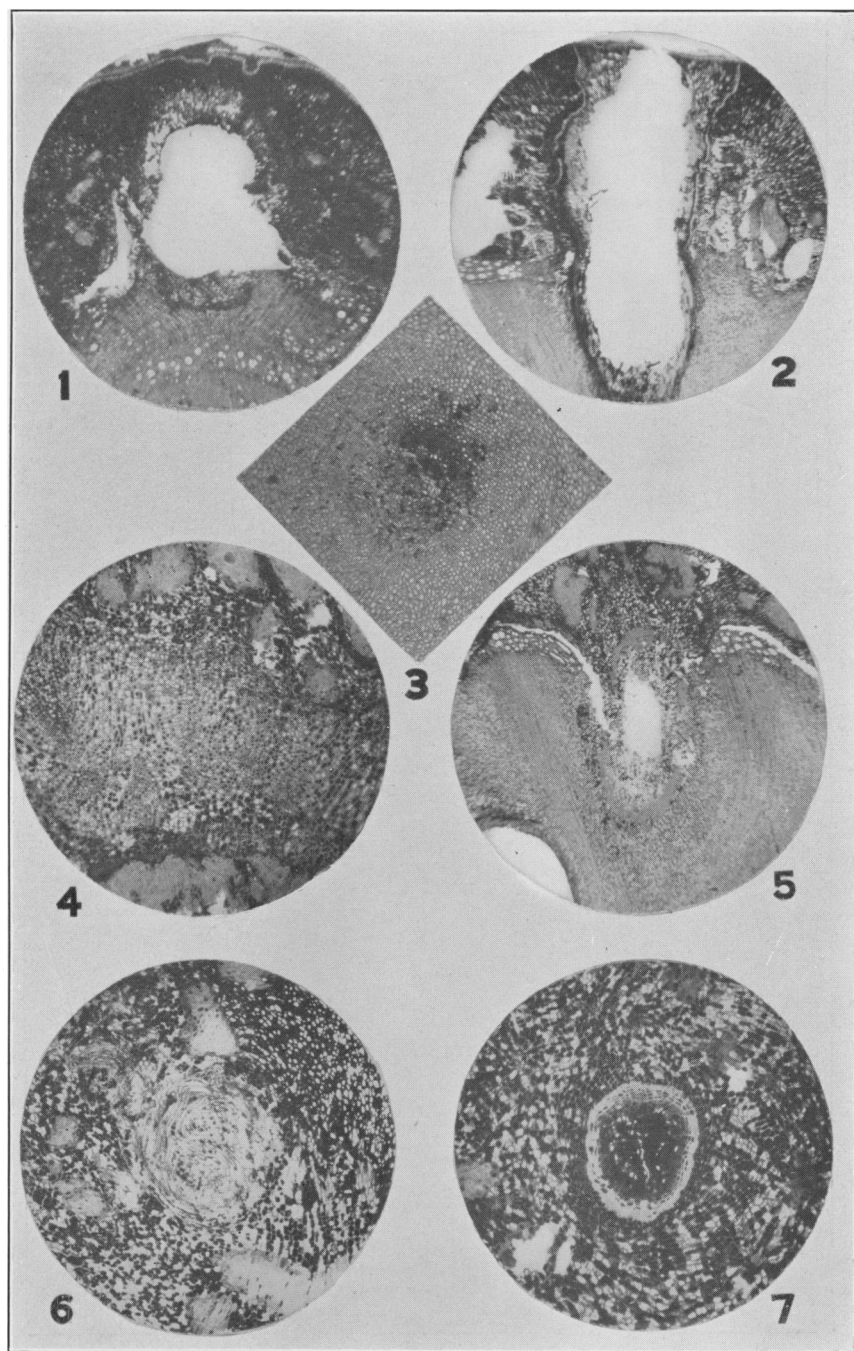
FIG. 10. External view of the punctatus gall. Openings to chambers shown by dark dots. $\times$ about $\frac{1}{2}$.

FIG. 11. Tangential section through a portion of the stem below gall showing nearly normal ray structure. Photograph taken from same section as part shown in figure 9. $\times 33$.

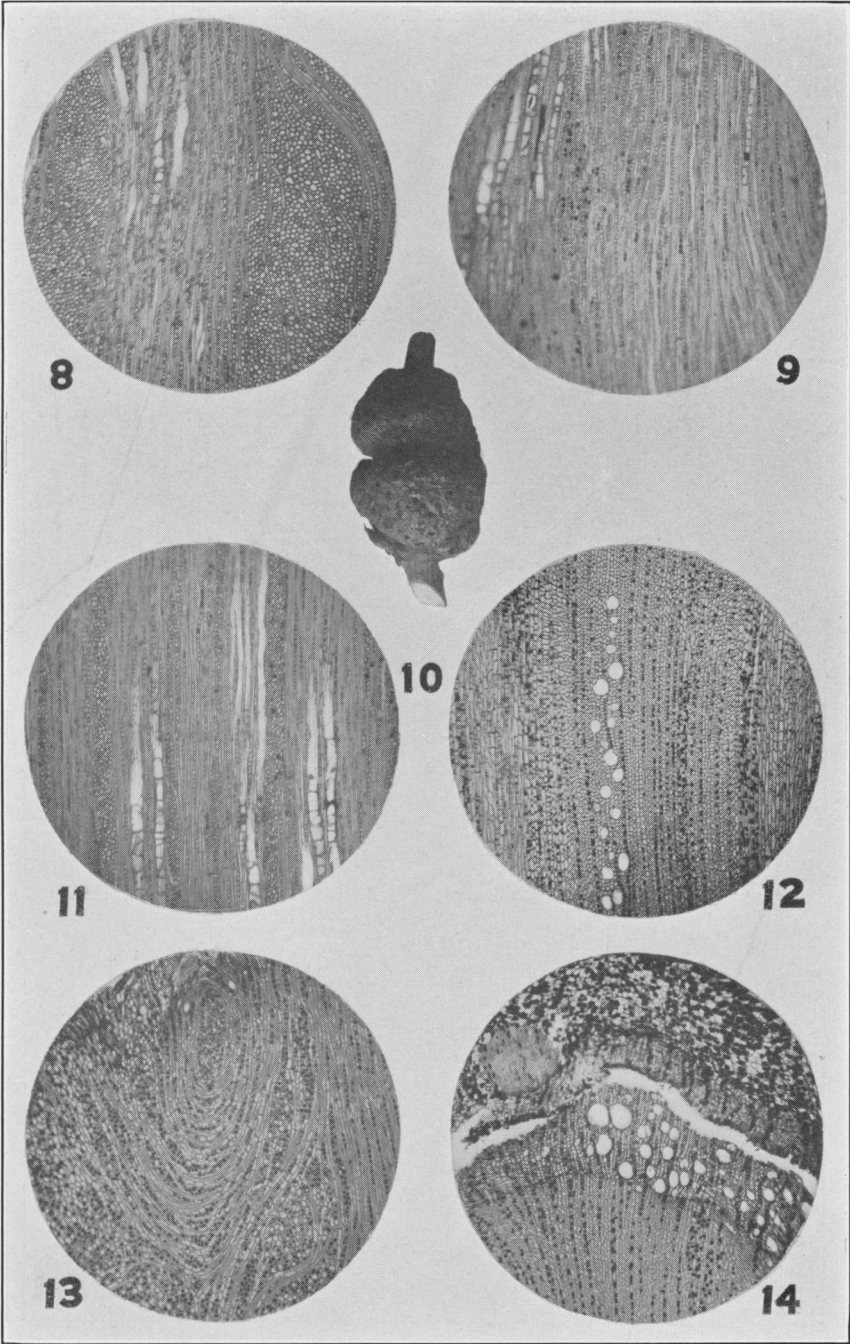
FIG. 12. Cross section of a portion of a gall showing radial sector containing vessels in the wood of the gall. $\times 33$.

FIG. 13. Tangential section showing ball-formation (Knäuel) in wood of gall. $\times 33$.

FIG. 14. Cross section of a portion of an old gall showing apparent return to normal growth. The light line across the figure is caused by a slight separation of the wood and bark at the cambium. $\times 33$.



STEWART: ANATOMY OF THE PUNCTATUS GALL.



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